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Spatio-temporal Distribution and Food-searching Strategy Differentiations between Two Silphid Beetles, *Eusilpha japonica* and *E. brunnicollis* (Coleoptera, Silphidae)

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Abstract To understand the interspecific interaction between *Eusilpha japonica* and *E. brunnicollis*, we investigated their spatio-temporal distributions and food-searching strategies using baited traps in southern Kantô, Japan. In spatial distribution, more *E. japonica* lived in managed forest and grassland than in unmanaged forest, but more *E. brunnicollis* lived in forest margins than in grassland. However, the abundance of the latter species showed no clear tendency with regard to whether the forest was managed or not. In temporal distribution, both beetles were collected mainly from May to August, although their peaks of abundance differed; *E. japonica* peaked in May to June and in August, while *E. brunnicollis* peaked in July. In food-searching strategies, *E. japonica* searched by walking, whereas more *E. brunnicollis* searched by flying than by walking. Thus, *E. japonica* and *E. brunnicollis* partly differed not only in spatio-temporal distribution but also in food-searching strategies. These results suggest that interspecific competition for food may be slight between them, but it will occur.

Introduction

Although carrion is nutritionally rich, it is also small, distinct and ephemeral, and so attracted animals must become specialized to exploit this resource quickly (KENTNER & STREIT, 1990; HANSKI, 1990). Thus, carrion is a resource for which intense competition is expected. Indeed, several studies have reported the occurrence of severe competition among consumers of carcasses (*e.g.*, KNEIDEL, 1984).

Many beetles belong to the family Silphidae, which consumes carrion. Thus these beetles, particularly in the genus *Nicrophorus*, have been studied for their interspecific interactions. Many studies about interspecific interactions have focused on spatio-tem-

poral distribution (ANDERSON, 1982; SHUBECK, 1983; KATAKURA & UENO, 1985; BENINGER & PECK, 1992; BENINGER, 1994; LINGAFELTER, 1995). Some studies showed overlapping spatio-temporal distributions and intense interspecific competition among species (WILSON *et al.*, 1984; TRUMBO, 1990; SCOTT, 1994; OHKAWARA *et al.*, 1998; SUZUKI, 2000). However, far fewer ecological studies about other silphid beetles have been undertaken.

Reproductive ecology and behavior of *Eusilpha japonica* and *E. brunnicollis* are much similar in laboratory observation (KIMURA, 1995; NAGANO, 2003). Both of them show no parental care same as other Silphinae, the females deposit their eggs in the soil one by one (KUROSA, 1959; HARUSAWA, 1996 about only *E. brunnicollis*) and leave there as soon as they oviposited (KIMURA, 1995; NAGANO, 2003). Both larvae hatch within four days at 20°C (NAGANO, unpublished data) and then search for food on the ground by oneself (NAGANO, 2003). Their foods are small and large vertebrate and invertebrate carcasses (KUROSA, 1959; NAGANO, 2003). They pupate in the soil after the third ecdysis in less than 15 days from the time they hatched, and the pupal stage is 15–20 days at 20°C (NAGANO, unpublished data). Similar to the larval stage, behavior and food habit of adult *Eusilpha japonica* and *E. brunnicollis* is alike (KIMURA, 1995; NAGANO, 2003). They not only feed on carcass but live on invertebrates such as fly maggots.

In Honshu, Japan, the distributions of *Eusilpha japonica* and *E. brunnicollis* sometimes overlap (ITO & AOKI, 1983; KUROSAWA, 1985), so that it is possible that they compete for foods. Thus, to investigate the spatio-temporal distributions and food-searching strategies of these organisms, we selected four different habitats at two sites in southern Kantô, Japan, and set two types of bait traps during the period from March to November. In addition to an analysis of the results, we discuss the interaction among *Eusilpha* beetles and nicrophorine beetles (Silphidae, *Nicrophorus* and *Ptomascopus*).

Material and Methods

Study sites

The study was conducted in the Tama Forest Science Garden (TFSG), Hachiôji, Tokyo Metropolitan, and in the Yokohama Nature Sanctuary (YNS), Yokohama, Kanagawa Prefecture. Both areas are located in the southern Kantô region, Central Japan, which belongs to the warm-temperate climate zone. We selected four different stations in both sites, and set traps with putrefied chicken meat (6 days in last 10 days of each month). The study in TFSG was conducted from October to November in 1998, and from March to September in 1999; in YNS, from April to November in 1998 and in March in 1999. The environment of each station was as given below.

Tama Forest Science Garden (*TFSG*)

This area is located at the foot of Mount Takao (lat. 35°39′N, long. 139°17′E,

elev. about 200 m, average annual temp. 14°C). The majority of this area is covered with an artificial forest, but primary forest remains in some portions (about 13 ha). We placed one station in a primary forest (T1) and three stations in artificial forests (T2–4).

T1: (Primary forest). Dominant trees were oak, *Quercus acuta*. Dominant shrub tree was Japanese aucuba, *Aucuba japonica*. Undergrowth was sparse. The litter layer was thicker than 6 cm.

T2: (Unmanaged forest). Dominant tree was oak, *Q. myrsinaefolia*. These trees were planted more than 70 years ago, and have not been managed. Dominant shrub tree was Japanese aucuba. Undergrowth was sparse. The litter layer was thicker than 6 cm.

T3: (Managed closed forest). Planted trees were diverse; there was no dominant tree, most of these trees were shorter than 8 m and the canopy was almost closed. Due to annual mowing there was almost no shrub layer, but herbs (mostly lilies, *Ophiopogon japonicus* and *Liriope muscari*) grew abundantly. The litter layer was thinner than 5 cm.

T4: (Managed open forest). Like T3, various trees were planted in this station; there was no dominant tree, though the trees are taller than 12 m, tree density was low and partly the canopy was open. Shrub layer was almost absent due to mowed annual mowing and undergrowth was abundant (mostly lilies, *O. japonicus* and *L. muscari* with some lianas). The litter layer was thinner than 3 cm.

Yokohama Nature Sanctuary (YNS)

This site is located at the base of the Miura Peninsula at the foot of Enkai-zan (lat. 35°20′N, long. 139°35′E, elev. about 100 m, annual average temp. 15°C). The vegetation is a mainly deciduous broad-leaved secondary forest, though the potential primary vegetation is temperate evergreen broad-leaved forest. Such primary vegetation has survived in only small portions of the area.

Y1: (Inner secondary forest). This station was situated at least 50 m removed from the forest margin. Dominant tree was oak, *Quercus serrata*. Dominant shrub was Japanese aucuba, *Aucuba japonica*. Most of the undergrowth was lilies, *Ophiopogon japonicus* and *Liriope muscari*. The litter layer was thicker than 5 cm.

Y2: (Secondary forest near margin). This station was 2–5 m apart from the forest margin. Dominant tree was also oak, *Q. serrata*, and dominant shrub was Japanese aucuba, but the tree density was lower and the shrub density was higher than at Y1. There were many saplings such as *Q. acuta*, *Ilex integra* and *Cinnamomum japonicum*. Undergrowth plants were not abundant. The litter layer was thicker than 4 cm.

Y3: (Grassland near forest margin). This station was between the secondary forest and a road, being approximately 10 m apart from both the forest and road. There were few trees and no shrubs due to mowing every late autumn, but grasses such as Japanese pampas grass, *Miscanthus sinensis* and goldenrod, *Solidago altissima* were abundant in spring through autumn. The litter layer was thinner than 3 cm.

Y4: (Grassland). There were neither trees nor shrubs for the same reason as Y3, but grass coverage was thick. The dominant grasses were the same as Y3. Litter was almost absent.

Sampling

Beetles were trapped in aluminum cans (length: 16.5 cm, diameter: 6.5 m, diameter of opening: 2.0 cm) with two holes (about 0.2 cm) at the bottom to drain. A piece of fresh chicken meat (about 20 g) was placed in each can as bait. Two types of traps were set. One was so buried as its rim was level with soil surface, and covered with square cardboard (about 15 cm in length, about 10 cm above the opening) to protect the trap from rainfall and also as marking. Other traps were hung from trees using fishing line at a height of 1.5–2.0 m above the ground. In each station, 10 ground traps and 10 hung traps were set alternately, at least 20 m apart from each other and in as straight a line as possible. However, in the TFSG stations, from June to September, twelve to fifteen ground traps were set because many ground traps were destroyed by vertebrate scavengers. In total, 768 traps were set and, 673 traps were recovered in TFSG, and 720 traps were set and 660 of them were recovered in YNS. All traps were opened for six days and beetles were collected on the last day. Collected adult beetles were identified and counted. After recording, most beetles were released at their station of capture, but some were brought to the laboratory to measure their pronotal width and sex. Although larvae were captured by ground traps, they were released without recording.

Results

In both TFSG and YNP, *Eusilpha japonica* (MOTSCHULSKY, 1860) and *E. brunnicollis* (KRAATZ, 1877) were collected. The total number of *E. japonica* was 1468 and that of *E. brunnicollis* was 92 in TFSG; and 1629 *E. japonica* and 93 *E. brunnicollis* in YNS. The pronotal width of female *E. brunnicollis* was significantly smaller than that of male *E. brunnicollis* and that of *E. japonica* (Table 1, one-way ANOVA, Scheffé's method, d.f.$=3$, $F=20.0$, $P<0.05$), whereas other combinations showed no significant difference.

Table 1. Pronotal width.

Species	Pronotal width mean±SD (N)	
	male	female
E. japonica	9.29 ± 0.25^{a} (24)	9.37 ± 0.39^{a} (29)
E. brunnicollis	9.09 ± 0.38^{a} (26)	8.62 ± 0.46^{b} (26)

Values with the same letters are not significantly different (one-way ANOVA, Scheffe's method, d.f.$=3$, $F=20.0$, $P<0.05$).

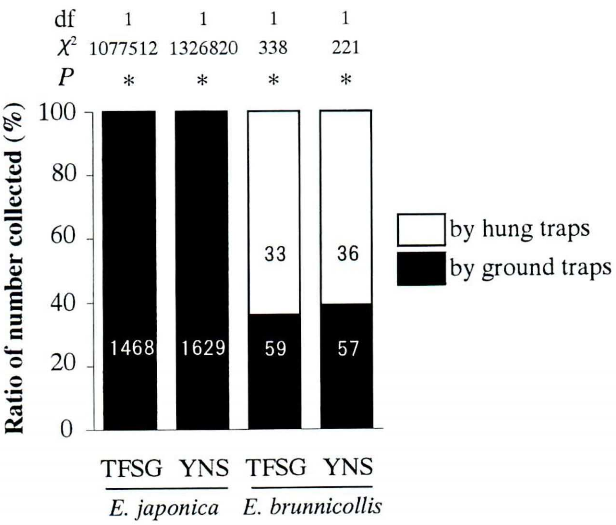

Fig. 1. Ratio of the number of beetles collected by hung traps to that collected by ground traps. Asterisks show significant difference at the 0.001% level by χ^2 test.

Differences in numbers collected between ground traps and hung traps

The ratio of numbers of the beetles collected between hung traps and ground traps is shown in Fig. 1. No *E. japonica* was collected by hung traps. On the other hand, the number of *E. brunnicollis* collected by hung traps was much larger than that by ground traps at both sites (χ^2 test, d.f.$=1$, $P<0.001$).

Habitat association

Figure 2 shows the habitat associations of *Eusilpha japonica* and *E. brunnicollis* in TFSG and YNS. The number of *E. japonica* was much smaller in primary forest (T1) and unmanaged forest (T2) than in managed forest (T3 and T4) in TFSG (one-way ANOVA, Scheffé's method, d.f.$=3$, $F=18.0$, $P<0.05$), and it was much smaller inside the forests (Y1 and Y2) than outside (Y3 and Y4) in YNS (one-way ANOVA, Scheffé's method, d.f.$=3$, $F=16.9$, $P<0.05$). On the other hand, the number of *E. brunnicollis* was much smaller in managed closed forest (T3) than in unmanaged forest (T2) or managed open forest (T4) in TFSG (one-way ANOVA, Scheffé's method, d.f.$=3$, $F=4.9$, $P<0.05$), and it was much larger in secondary forest near the margin than in inner secondary forest (Y1) or grassland (Y4) in YNS (one-way ANOVA, Scheffé's method, d.f.$=3$, $F=5.0$, $P<0.05$).

Seasonal activity

Seasonal fluctuations in the numbers of collected beetles are shown in Fig. 3. The fluctuations in *Eusilpha japonica* and *E. brunnicollis* were significantly correlated between TFSG and YNS (Spearman's correlation coefficient, *E. japonica* $r_s=0.98$,

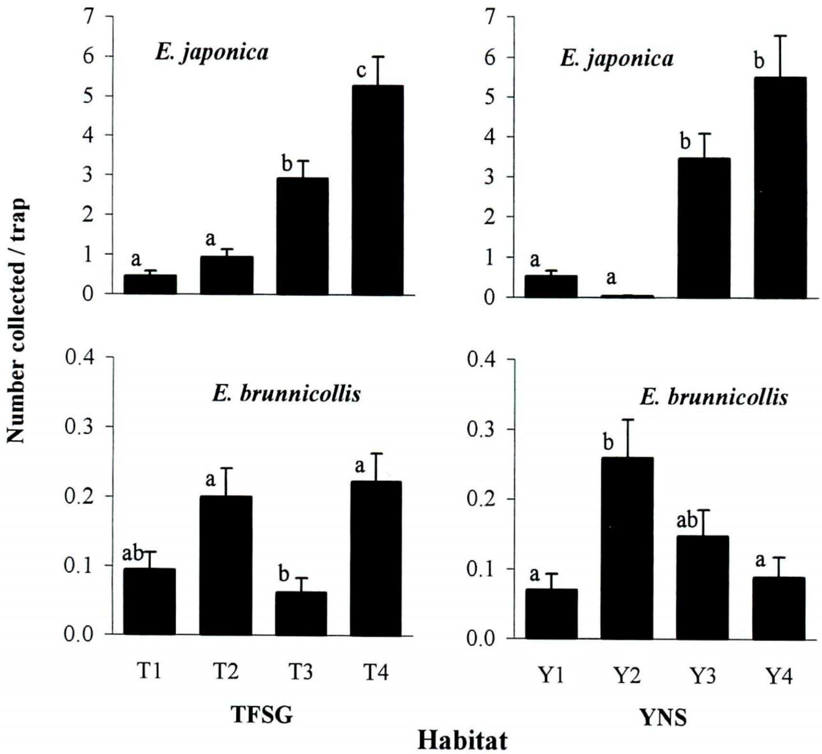

Fig. 2. Number of beetles collected per trap in each habitat. Values with the same letters are not significantly different (one-way ANOVA, Scheffé's method, $P<0.05$). Vertical bars illustrate +SE.
TFSG: T1=Primary forest, T2=Unmanaged forest, T3=Managed closed forest, T4=Managed open forest.
YNP: Y1=Inner secondary forest, Y2=Secondary forest near margin, Y3=Grassland near forest margin, Y4=Grassland.

$P<0.01$; *E. brunnicollis* $r_s=0.82$, $P<0.05$). *Eusilpha japonica* was collected from April to October with two activity peaks in May to June and August in TFSG; in YNS, collection was from May to October with two peaks in May and August. *Eusilpha brunnicollis* was collected from April to October with a single peak in July in TFSG, and from May to October with a peak in July in YNS.

Discussion

The spatio-temporal distributions differed between *Eusilpha japonica* and *E. brunnicollis*. In spatial distribution, more *E. japonica* lived in managed forest (T3 and T4) and open land (Y3 and Y4) than in unmanaged forest (T1, T2, Y1 and Y2). On the other hand, more *E. brunnicollis* in YNS lived in forest margins (Y2, Y3) than in inner forest (Y1) or grassland (Y4). However, the abundance of *E. brunnicollis* in TFSG

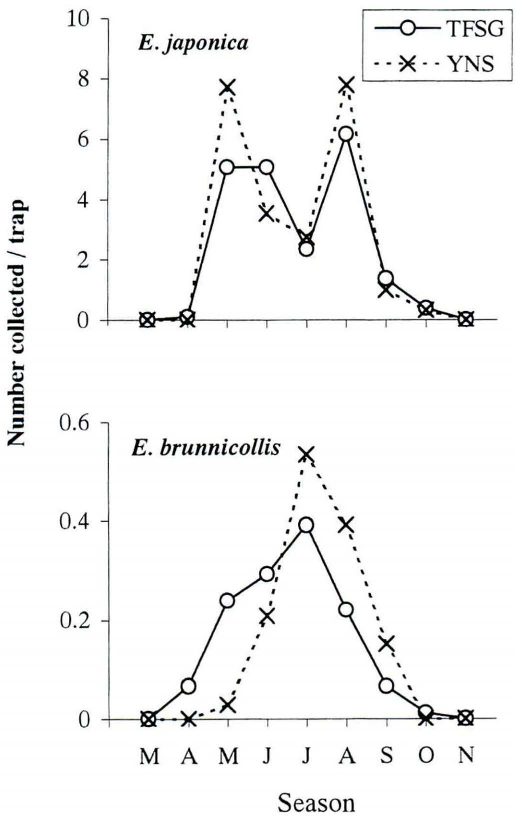

Fig. 3. Seasonal fluctuations in numbers of beetles collected.

showed no clear tendency with regard to whether a forest was managed or not (Fig. 2). In temporal distribution, both *E. japonica* and *E. brunnicollis* were collected mainly from May to August, while the peaks of their abundance differed: *E. brunnicollis* peaked in July, when *E. japonica* was off-peak (Fig. 2). However, there was much greater abundance of *E. japonica* than *E. brunnicollis* in all active seasons and in all habitats, except for Y2 in July. We suppose that the reason of *E. japonica* exceedingly dominant over *E. brunnicollis* is the difference of their eating habits. ITO and AOKI (1983) reported that *E. brunnicollis* disappears with urbanization. In contrast, *E. japonica* inhabits through forest area to urban area (small grassland in urban). AOKI (1996, 2000) mentioned that many urban animals have wide food niche. Then, eating habits of *E. japonica* may be wider than that of *E. brunnicollis*. If this assumption is valid, the food of *E. japonica* is more abundant than that of *E. brunnicollis* in the same habitat. However, KIMURA (1995) and NAGANO (2003) reported that their food habitats overlapped in laboratory observation. And this study showed their spatio-temporal distributions largely overlapped but differed to some extent. Therefore, interspecific com-

petition for food may be only slight between *E. japonica* and *E. brunnicollis*, though it may occur.

Eusilpha japonica was caught by ground traps only, whereas more *E. brunnicollis* was caught by hung traps than by ground traps (Fig. 1). However, *E. japonica* can fly, since it has developed hind wings similar to those of *E. brunnicollis*. Indeed we observed *E. japonica* flying at height of 50 cm above the ground in Yokohama, Kanagawa Prefecture. These results show differences between *E. japonica* and *E. brunnicollis* not only in spatio-temporal distributions but also in food-searching strategies.

In the same place and using the same methods as the present study, NAGANO and SUZUKI (submitted) studied on spatio-temporal distribution of nicrophorine beetles (Silphidae, *Nicrophorus* and *Ptomascopus*). Nicrophorine beetles also feed on carrion, and *Nicrophorus* beetles demonstrate elaborate parental care behaviors, such as burying small vertebrate carcasses, building nests, feeding larvae and protecting both the carcasses and the larvae from aggressive intruders and predators until the larvae leave to pupate (*e.g.*, PUKOWSKI, 1933; SCOTT, 1998). NAGANO and SUZUKI (submitted) showed that three *Nicrophorus* species (*N. maculifrons*, *N. quadripunctatus*, and *N. concolor*) abound in unmanaged forest (T1, T2, Y1 and Y2) and rarely inhabit managed forest (T3 and T4) or open land (Y3 and Y4). Thus, *Eusilpha japonica* and *Nicrophorus* beetles were segregated spatially. *Eusilpha japonica* probably shifts their habitat to open land in order to avoid competition with *Nicrophorus* species, because *E. japonica* was abundant even in unmanaged forest in Kantô, where *Nicrophorus* species were absent (NAGANO, unpublished data). On the other hand, *Ptomascopus morio* mainly inhabits managed closed forest (T3) and forest margin (Y2, Y3), rarely inhabiting managed open forest (T4) or grassland (Y4). Their seasonal peak was in August (NAGANO & SUZUKI, submitted). Thus, *P. morio* and *E. japonica* partly overlapped spatio-temporally, and interspecific competition may occur between them.

To prove competitive interaction between *Eusilpha japonica* and *E. brunnicollis* or *Eusilpha* beetles and nicrophorine beetles, further investigation is needed, such as studies into their natural history and in particular, their reproductive strategies and larval food habits.

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要　　約

永野昌博・鈴木誠治：オオヒラタシデムシとベッコウヒラタシデムシの時空的資源利用様式の違い．—— オオヒラタシデムシとベッコウヒラタシデムシの種間関係を明らかにするために，両種の環境選好性，季節消長および餌探索法について調べた．その結果，オオヒラタシデムシは自然林や人為的管理が少ない森よりも草地や管理された森に多く生息していた．ベッコウヒラタシデムシは林縁で生息数が多くなる傾向がみられたが，森の管理による影響はみられなかった．両種とも5月から8月に活動していたが，オオヒラタシデムシは5月から6月と8月がそのピークであったのに対し，ベッコウヒラタシデムシではオオヒラタシデムシの活動が低下する7月に活動ピークがみられた．オオヒラタシデムシは地表を歩いて餌を探していたのに対し，ベッコウヒラタシデムシは飛行しながらも餌を探していた．以上のことから，オオヒラタシデムシとベッコウヒラタシデムシは，時間的一空間的に重複して活動しながらも，それらの中心的活動域および餌探索方法を違え，競争を軽減させていると考えられた．

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